XII. *On the Anatomy of* Nautilus umbilicatus, *compared with that of* Nautilus Pompilius. *By* JOHN DENIS MACDONALD, *R.N., Assistant-Surgeon of H.M.S.V. 'Torch,' commanded by Lieut.* WILLIAM CHIMMO, *R.N., tender to H.M.S. 'Herald,' Captain* H. M. DENHAM, *R.N., F.R.S., commanding the Expedition to the South Seas. Communicated by Sir* WILLIAM BURNETT, *K.C.B. &c.*

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HER Majesty's Steam-Vessel 'Torch' having visited the Isle of Pines in the month of July 1854, one of the officers had the good fortune to pick up a recent specimen of *Nautilus umbilicatus* on the outer reef off Observatory Island. The creature had most probably been thrown up by the waves, and remained within a ledge of coral when the spring tide receded. The natives frequently find *Nautili* entrapped in this way, but we could not prevail upon them to bring us the recent animals, although a liberal remuneration was offered.

The specimen forming the subject of the present paper was alive when brought on board, but it was too much exhausted to exhibit any active movements when placed in a vessel containing sea-water. On touching the tentacula they curled up, or moved about irregularly, and the muscular fibres of the funnel lobe contracted slowly, without however producing respiratory currents.

A considerable portion of the posterior part of the hood appeared to have been eaten away by some predaceous enemy, but in other respects the animal was perfect.

On comparing the *Nautilus Pompilius* with *Nautilus umbilicatus* in the recent state, besides the remarkable differences existing between their respective shells, one is struck with the deep position of the latter animal when fully retracted, the space between the upper surface of the hood and the lip of the shell being so considerable, that in the lateral view no part of the creature is visible. On the other hand, the animal of *N. Pompilius* completely fills the chamber of occupation, and many of the tentacula, with a large portion of the hood, rise above the peristome of the shell, so that when the soft parts are removed the rounded orifice of the siphuncle may be distinctly seen in the last-formed septum. Not so however with *N. umbilicatus*; on account of the great depth of the chamber in which the animal is lodged, the opening of the siphuncle cannot be seen in the empty shell. It must be remembered, however, that when a new septum is formed, the last chamber is comparatively shallow, and it continues to deepen as new additions are made to the lip of the shell until the development of another septum is necessitated.

Apart from the shells, these two species, if indeed they may be considered distinct, so

closely resemble each other as to render it very much easier to trace out their similarity in corresponding parts, than to determine essential differences between them.

The specimen of *N. umbilicatus* examined proved to be a female, a fact which may serve to modify the views of those who, adopting the ingenious speculations of D'Orbigny with reference to the sexes of the Ammonites as indicated by the characters of their shells, apply them also to the several kinds of *Nautili* known. The numbers of the different tentacula in this example, as represented in the following table, agree sufficiently well with those of *N. Pompilius* already recorded; considering the liability of these organs to exhibit slight modifications in form, arrest of development, or supernumerary parts on one or both sides.

Numerical Table of the Tentacula.

	Left side.	Right side.	Total.
Digital tentacula	19	19	38
External labial tentacula ...	12	12	24
Internal labial tentacula ...	12	12	24
Ocular tentacula	2	2	4
Total	45	45	90

As it is not my intention to enter into an elaborate description of the whole anatomy of *N. umbilicatus*, seeing that in so doing I should be needlessly repeating all those particulars so succinctly detailed by Professor Owen with respect to the *N. Pompilius*, I therefore purpose making some observations on the microscopic anatomy of the organs of the special senses, and the glandular follicles appended to the four vessels which convey the blood from the sinus-system to the branchiæ; and in the explanation of the figures, I shall note as they occur, all the more important matters bearing on the question as to whether the *N. umbilicatus* is to be regarded simply as a variety of *N. Pompilius*, or as an originally distinct species.

Organ of Vision.—To my former observations on the minute anatomy of the eye in *N. Pompilius* I have little more to add, as they are alike applicable to *N. umbilicatus*. I am more fully satisfied than ever that the pigmentary coating is subjacent to the retina, and that the filamentous ends of the fusiform cells of the former commingle with the finely granular and vesicular matter of the latter. I have reason to believe also that the long axes of the pigment-cells themselves are perpendicular to the surface of the retina, like the club-shaped bodies of Jacob's membrane, and parallel examples to this are found in the eyes of some marine Annelidans.

I have not been able to trace a vestige of a lens, nor do I believe that such can exist; and the only representative of a vitreous humour is a kind of viscosity which appears to protect the retina from the direct action of the sea-water. The exterior of the eye (Plate XIV. fig. 1 *a*) was marked at the back part and in the region of the pupil with blotches of the same rich brown pigment which tinted the upper surface of the hood and a few of the tentacular sheaths.

Organ of Hearing.—The thorough investigation of the various systems and organs of an animal previously almost wholly unknown, with a single mutilated specimen at the disposal of the anatomist, is attended with difficulties which can only be surmounted by the accomplished dissector. An undertaking of this kind fell to the lot of Professor Owen when he entered upon the examination of the first recent Pearly Nautilus that reached the shores of England, and the beautiful monograph resulting from the right use of this single opportunity is a lasting memorial of the genius of its author. The organ of hearing seems to have been the only matter of any importance that escaped the scrutiny of the Professor, and although I have been fortunate enough, myself, to discover the auditory capsules in the recent *N. umbilicatus*, I can easily conceive the difficulty of detecting them in a specimen long preserved in spirits, which renders the tissues opaque and ill-adapted for microscopic investigation.

The acoustic capsules in my specimen were about one-twelfth of an inch in diameter, subspherical in form, and situated at the union of the supra with the subœsophageal ganglia, but more especially connected with the short pedicle of the anterior division of the latter (Plate XV. fig. 1 *d*). I have been induced to look for them in this locality, bearing in mind the condition of the organ of hearing in most Gasteropoda, and recognizing the close affinity of the Nautilus to this order.

In every instance the supra-œsophageal ganglia occupy the cephalic region, but on account of the great length of the neck and body anterior to the visceral nucleus in Heteropoda, the subœsophageal nervous masses suffer the maximum amount of backward displacement, and the whole nervous system approximates the homogangliate type. In this extreme case the ear is still preserved in the neighbourhood of the eye, and the special centres of vision and audition are incorporated with the supra-œsophageal ganglia, from which both the auditory and optic nerves arise.

The inner wall of each ear-sac in the Nautilus is somewhat flattened, lying in contact with the nervous matter; but its more convex external surface rests in a little depression on the upper and internal border of the cephalic cartilage. It is enveloped in a kind of fibrous tissue, and filled with a cretaceous pulp consisting of minute elliptical otokonia, which, when under a high power, present a bright and strongly refracting point near each extremity. These particles vary much in size, and are sometimes curiously combined, so as to appear double, or assume the form of a star or cross, &c.

This simple auditory apparatus may be readily exposed by making an incision externally in the deep groove between the funnel lobe and the basal part of the tentacular sheaths, immediately in front of the hollow subocular process.

The cilia lining an auditory sac containing minute otokonia, are always much finer than those required to impart a rotatory motion to a single spherical otolithe. I have not observed them in the ear of the Nautilus, although I cannot for a moment doubt their existence.

VALENCIENNES traced three small nervous filaments into a cavity of the cephalic cartilage, which he says was filled with a homogeneous pulp, and did not contain any kind of concretions; but not having had the opportunity of perusing his original memoir on the *N. Pompilius*, in which animal he observed this structure, I cannot determine with any degree of certainty the parts to which he refers. From my own observation, I can scarcely imagine that the nature of the venous sinus, which excavates the cephalic cartilage on either side, could be mistaken by a well-informed anatomist, and yet there is much probability in the suggestion of Professor OWEN, that this is the locality to which VALENCIENNES assigns the organ of hearing.

As our knowledge of the Mollusca advances, the localization of the special centre of audition, as well as the nature of the contents of the simple capsules, which shadow forth the vestibule of the more perfect apparatus of hearing, will prove of great importance to the natural classification of these animals. Thus, even with respect to the contents of the capsules, we find spherical otolithes present in the Heteropoda, Pectinibranchiata and several other orders; and otokonia in the Pulmonifera, and as far as I have been able to discover, except while yet in their embryonic state, in the whole of the Pteropoda, including PERON's *Phyllirhoë*, which is more closely allied to these last than to the Gasteropoda. Now as we know that the ear-chambers in the dibranchiate Cephalopoda contain single otolithes of large proportional size, although this rule may not be general in its application, it would not be unreasonable to conclude, from the evidence afforded by the Nautilus, that the auditory sacs of the extinct Tetrabranchiata were distended with minute pulverulent otokonia.

Organ of Taste.—Although a doubt may still exist as to the locality of the olfactory sense in the Nautilus, this can hardly be said of the organ of taste, the mucous membrane of the mouth is so richly supplied with sentient papillæ. These bodies are distributed in three principal groups; thus a considerable number beset a stout vertical fold of the lining membrane, extending, on either side, from the root of the tongue to the back of the pharynx. The papillæ are more numerous on the inner side and along the free border of each fold, in order to give them a greater extent of motion and render them opposable to the remaining group (Plate XV. fig. 4 *b*), which occupies the median line, between the orifice of the tongue-sac, *a*, and the commencement of the œsophagus, *e*; and although placed a little posterior to the organ usually recognized as the tongue in the higher Mollusca, they may with great propriety be named the lingual papillæ, to distinguish them from the others. All the papillæ agree, however, in their general character and minute anatomy, being either simple or compound, exhibiting much irregularity in form, and being clothed with long and delicate columnar epithelial cells, the homogeneous basement membrane enveloping a kind of areolar tissue.

Renal Organs.—It is reasonable to suppose that an animal possessing a complex digestive system for the reduction of crude animal matter, should be also furnished

with renal glands, to separate from the blood those deleterious principles which must otherwise accumulate. In the Nautilus there are no organs to which this function can be more justifiably assigned than the numerous glandular follicles appended to the vessels which convey the blood from the sinus system to the branchiæ; admitting also that by altering their capacity they may serve to regulate the amount of blood circulating through the respiratory apparatus under those changes of pressure which the animal must experience in sinking to great depths and rising in its watery element. MAYER suggested that the homologues of these follicles in the higher Cephalopoda were the emunctories of the urine, and Professor OWEN considers it more philosophical to conclude that the organs of so important an excretion should be present in all the class, than that they should be represented by the ink-gland and bag which are peculiar to one order. As the most satisfactory method of arriving at a just conclusion, however, I shall leave further argument for the present, and describe the minute anatomy of the organs, which may be provisionally called the renal follicles of the Nautilus.

These follicles are subcylindrical in form, somewhat dilated at the free extremity, to which is appended a folded and funnel-shaped process of membrane, which expands rather suddenly, presenting a jagged and irregular border. They open by a smooth and oral or slit-like orifice into the afferent pulmonary vessels, on each of which, as Professor OWEN has observed, they are disposed in three clusters.

The outer membrane is smooth and glossy, homogeneous in structure, and sprinkled over with minute rounded and transparent bodies, probably the nuclei of cells. Beneath this layer flat bundles of fibres, apparently muscular, are traceable here and there, principally disposed in a longitudinal direction, and sometimes branched.

The lining membrane consists of a loose epithelial pavement, in many respects similar to that of the uriniferous tubules of the higher animals; the cells containing, besides the nuclei, numerous minute oil-globules, or a substance much resembling concrete fatty matter.

This membrane is thrown up into an infinite number of papillæ and corrugations, so as to augment the extent of surface considerably. The papillæ are more numerous at the inner part, or towards the attached end, and a circlet of longitudinally disposed folds radiate from the bottom of the follicles, in which a number of small pits or fenestrations is sometimes visible. The sides of these folds are wrinkled transversely, so as to present a median zigzag elevation.

The funnel-shaped membranous process above noticed is continuous with the lining membrane, consisting of an extension of the same epithelial pavement, but the cells are somewhat larger and more regular in form. The cavity of each follicle, therefore, communicates with the exterior through the centre of this process, and the aperture is thus guarded by a kind of circular valve, permitting the escape of secreted matters, but effectually preventing the entrance of fluid from without.

Now that grave doubts have been cast upon the existence of the so-called epithelial investment of the Malpighian tufts of the kidney in Vertebrata, the office of these minute vascular bodies would seem to present a solitary example of the secretion of a peculiar fluid directly from the blood, or independently of the agency of nucleated cells. The glandular follicles of the Nautilus just described appear, as it were, to go one step further, the vascular and secreting portions having so far coalesced as to be almost undistinguishable the one from the other. When the Malpighian tufts are excessively distended with the contained blood, the albuminous elements pass away with the thinner parts, and doubtless congestion of the renal follicles of the Nautilus would be attended by a similar result*.

These views may be still further supported by glancing at the relationships of the kidney, liver, and respiratory organs in the Vertebrata and Mollusca respectively. Thus, in vertebrate animals the biliary fluid is secreted from venous blood supplied by the portal system. In Mammals the secerning vessels of the kidney are chiefly arterial; but in Fishes, which possess a distinct portal system in connexion with the kidney, the urine is principally separated from venous blood, which ultimately commingles with that returning from the liver before reaching the *branchial* heart.

In Mollusca, on the contrary, the biliary secretion is furnished from arterial blood; and if the glandular follicles of the Nautilus above noticed are veritable renal organs, as they evidently appear to be, the kidney exchanges place, as it were, with the liver, lying between the great sinus system and the branchiæ, which return their blood into a *systemic* heart.

It will be perceived, therefore, that in these respects a remarkable difference exists between the Mammalia and Mollusca; but the steps of transition from the one to the other are so distinctly marked in the intervening classes, taken in their natural order, that we are enabled more fully to comprehend the nature of this disparity; the apparently anomalous position of the renal glands in Nautilus and Sepia, and indeed also in certain Gasteropoda and Conchifera, in which their function has been more satisfactorily determined, being reconciled with the relative anatomy of those organs in animals of higher grades.

The body of *N. umbilicatus* is larger and more elongated than that of *N. Pompilius*, as it occurs in the South Seas, although the specimens of the latter species brought from the Chinese Seas much exceed both in size. In the *N. umbilicatus* the longitudinal lamellæ on the median lobe of the external labial processes are divided by a wide groove into two distinct lateral sets, and the corresponding lamellæ between the internal labial processes are about seventeen in number and of considerable thickness. In *N. Pompilius* the latter lamellæ are much thinner and more numerous, and the lateral sets of the former are united together in the median line,

* On comparing these follicles with their spongy homologues in *Sepia*, for example, one cannot fail to observe in them a relationship similar to that existing between the lobulated renal organ of the Porpoise and the more condensed and perfect kidney of Man.

commencing anteriorly with an azygos transverse lamina. In both kinds, however, I have distinctly traced out the corresponding tentacula, with such minor differences as might be expected to occur in different specimens of either separately. The question here naturally arises,—Are the peculiarities observable in the descriptive and microscopic anatomy of each of sufficient importance to entitle them to be considered distinct species, or are they within the pale of that latitude which must be allowed to variety?

Any tendency in a being to revert to an original type, when such has been determined, betrays variety; but this tendency in the *Nautili* now under consideration is never manifested by the occasional occurrence of specimens presenting characters which place them intermediate between *N. Pompilius* and *N. umbilicatus*.

Having visited the Fijii Islands since my former paper on the *N. Pompilius* was written, I find that the umbilicated *Nautili* are not known to the natives, although *N. Pompilius* is very plentiful; but at Fatuna or Wallis's Island, where both are found, the people recognize the difference between them, depending upon the presence or absence of umbilical pits. Now, although particular localities, with all attending circumstances, may favour the production of varieties, yet the permanence of the distinctive characters of these *Nautili* without symptom of amalgamation, and the discovery of a female specimen of *N. umbilicatus*, strongly support the view that they are distinct species, though very closely allied.

Explanation of the Plates.

PLATE XIV.

Fig. 1. Left lateral view of *N. umbilicatus* removed from the shell.

a. Eye.
b. Hood.
c. Tentacular sheaths.
d. Digital tentacula.
ee. Ocular tentacula.
f. Subocular hollow process.
g. Funnel lobe.
h. Mantle.
i. A lobe of the mantle which rests upon the black-stained patch of the shell.
j. A process similar to the last, beneath which it lies in the hollow of the hood, being continuous with the portion or part of the funnel lobe.
k. Shell-muscle.

l. Root of siphuncle. A small vessel may be seen coursing round it inferiorly.

The following parts are indistinctly visible through the mantle :—

m. Nidamental gland.

n. Chamber of pericardium, lodging the base of the ventricle of the heart, the branchial vessels and renal follicles.

A few globules of air are represented at the upper part of the chamber, having entered it by the sub-branchial openings, first described by Professor OWEN.

o. Gizzard.

p. Ovary.

Fig. 2. Simple dissection of the Nautilus, exposing all the more important parts of its anatomy, disturbed as little as possible from their natural relations.

a. The eye slit open in the vertical direction, showing the opalescent retina spread over the pigmentary layer. The subocular hollow process is seen projecting from the base of the eye-pedicle, immediately above the cephalic cartilage *f*, which appears in section.

b. Hood.

c. Tentacular sheaths.

d. Tentacula.

e. Funnel lobe. *e'*. Process corresponding to *j*, fig. 1.

f. Cephalic cartilage in section.

g. Shell-muscle.

h. Mantle. *h'*. Process corresponding to *i*, fig. 1.

i. Buccal mass.

j. Nervous ring of cephalic ganglia encircling the œsophagus and the terminal branches of the principal vessel. The long visceral nerves are seen passing in the interspace between the shell-muscles, to which a number of short radiating branches are distributed.

k. Dilated portion of œsophagus forming a kind of cross.

l. The gizzard.

m. Sacculated portion of stomach below the gizzard, receiving the large biliary duct, conveying thither the secretion of the three principal portions into which the liver is divided.

n, *n'*, *n''* respectively, the left, right and middle mass of the liver.

o. Biliary duct of the right division of the liver which is brought down from its natural position on the right side of the cross, the smaller extremity lying in contact with—

p. Peculiar glandular-looking bodies connected with the cross by muscular bundles and cellular tissue.

q. The intestine, forming two principal flexures.

r. Branchiæ.

s. Nidamental gland.

t. Anterior wall of pericardium, laid open to expose the contained organs.

t'. Posterior wall of ditto.

u, *u'*. Anterior and posterior renal follicles separated by an induplication of the anterior wall of the pericardium. This fold also extends between the anterior and posterior branchial vessels of the corresponding side which pour their blood into

v. The ventricle of the heart. The elongated posterior part of this organ extends into the abdominal cavity, through an opening in the posterior wall of the pericardium, and passing beneath the oviduct, gives rise to the principal arterial trunk, which continues its course beneath the rectum and the middle portion of the liver, around which it turns, giving off numerous branches to the neighbouring parts, as represented in the figure. It next ascends between the left principal division of the liver and the cross, and coursing obliquely along the left side of the œosophagus, it ultimately reaches the posterior part of that tube, to which it gives one or two vessels, and terminates immediately beneath the supra-œsophageal ganglia in fine branches, chiefly supplied to the buccal mass. In this course it gives off numerous lateral vessels of small size to the roof and sides of the cavity in which it lies, and a more important branch winds round the glandular bodies *p*, and is distributed to the border of the mantle.

When the posterior conical portion of the ventricle of the heart appears beneath the rectum, a small duplicature of the investing membrane is seen connecting these parts; this fold, I believe, includes one extremity of the "elongated pyriform sac," first noticed by Professor Owen as arising near the base of the aorta and ending in the venous sinus.

w. Ovarium, laid open on the right side, to expose, *x*, the calyces, of various sizes, attached along its roof.

The corrugations of the lining membrane of the calyces are proportionately large or small, bearing relation to the size of these bodies.

The ovary in this case was distended with a plastic albuminous fluid of a rich amber colour, and a considerable quantity of it found its way into the cavity of the abdomen, through a

large oval opening in the anterior wall of the ovary, with a thickened puckered margin, at which the investing and lining membranes are continuous. The posterior wall of the pericardium, on the right side, acts as a valve to this opening.

Although I have observed the albuminous fluid just alluded to free in the abdominal cavity of *N. Pompilius*, I did not discover the orifice by which it must have escaped from the ovary.

z. The narrow oviduct is seen passing forwards on the right side of the rectum, and ending in a thickened and apparently glandular extremity, from the left side of which a fold of the investing membrane arches over the rectum near the termination of the long visceral nerves, lying below and in front of the reflected layer of peritoneum, which prevents the admission of the sea-water with the blood bathing the cephalic ganglia, œsophagus, and buccal mass. The lateral attachment of this layer is represented by faint lines on the inner surface of the shell-muscle, extending upwards and backwards to the apex of the left hepatic mass.

PLATE XV.

Fig. 1. Dissection exhibiting the auditory sac of the right side, inside *in situ*, the cephalic ganglia, neighbouring parts, &c.

a. The eye, beneath which is seen the hollow process resembling a tentacular sheath.

b. Supra-œsophageal nervous mass, cylindroid in form, and presenting a ganglioniform enlargement at either end, from which the optic nerves are given off. The stout fibrous envelope is slit open, exposing the reversed loops of four nerves which pass onwards to the buccal mass.

c. Posterior division of the subœsophageal ganglia, giving off from its convex border a considerable number of nerves to the shell-muscles, and, on either side of the median line, two principal visceral nerves.

d. Portion of anterior division of subœsophageal ganglia, with the auditory sac lying on the outer surface of its pedicle, near the point where all the principal cephalic nervous masses of the corresponding side unite. A small depression may be noticed on the upper and inner border of the cephalic cartilage in which the auditory capsule rests.

The funnel lobe, shell-muscles, and the principal artery running upon the œsophagus, giving it a small vessel and terminating in fine branches, which pass through the nervous ring towards the buccal mass, need no references.

Fig. 2. The auditory sac: natural size.

Fig. 3. The otokonia: highly magnified.

Fig. 4 exhibits the opening of the tongue-sac *a*, the lingual papillæ *b*, and those distributed upon the buccal folds of lining membrane *c*.

d. Semi-cartilaginous substance forming the matrix of the horny jaws, and affording attachment to muscles *f*.

e. Opening of the œsophagus.

g. Sublingual processes, the inferior one being detached from the corresponding jaw.

Immediately in front of the lingual papillæ, the mucous membrane forms two small wing-like folds, lying side by side, *h*, which serve to close the opening of the lingual sac; and a linear projection extends, from between them, along the roof of the sac, being impressed by the teeth of the rachis, and the internal series of uncini on either side. The microscopic structure of the supporting cartilage of the lingual strap is perfectly similar to that of *N. Pompilius*; and with the trifling difference, that the uncini of *N. umbilicatus* are a little shorter than those in *N. Pompilius*, the lingual ribbon, and I may also include the horny jaws of both, so nearly resemble one another as to render separate illustration quite unnecessary.

Fig. 5. A cluster of papillæ enlarged to show their general form and character.

Fig. 6. Tip of one of the papillæ, highly magnified to show the investing columnar epithelium. A considerable number of these almost filiform cells have been removed in order to display the rest more satisfactorily.

Fig. 7. Several of the renal follicles detached, with a portion of branchial vessel with which they were connected: natural size.

Fig. 8. Enlarged representation of the follicles seen at fig. 7, showing the funnel-shaped membranous processes appended to their free extremity, and the openings by which they communicate with the cavity of the branchial vessel.

Fig. 9. Crystalline bodies often occurring within the follicles.

Fig. 10. A few of the fibres which occasionally present themselves, disposed in flattened and branched bundles, between the external and internal coats of the follicles.

The remaining figures represent highly magnified portions of the lining membrane.

Fig. 11. Three of the zigzag longitudinal folds taken from the bottom of a follicle.

Fig. 12. A few of the hollow papillæ from near the attached end of ditto.

Fig. 13. Outer surface of a small fragment of the epithelial lining, showing the slit-like opening of a hollow process.

Fig. 14. Five cells of the same pavement, more highly magnified, to show the nuclei surrounded by minute fatty globules, reminding one of the condition of the epithelial cells of the human kidney in the early stage of BRIGHT's disease.

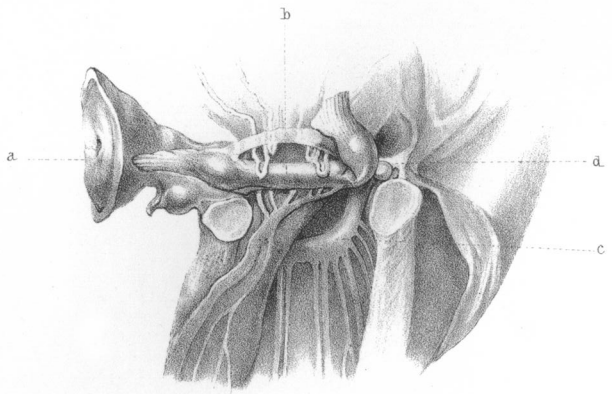
Fig. 1.

Fig. 2.

J. Macdonald, del. – J. Erxleben, lith.

Day & Son, Lith^rs to The Queen.

Fig. 1.



Figures.

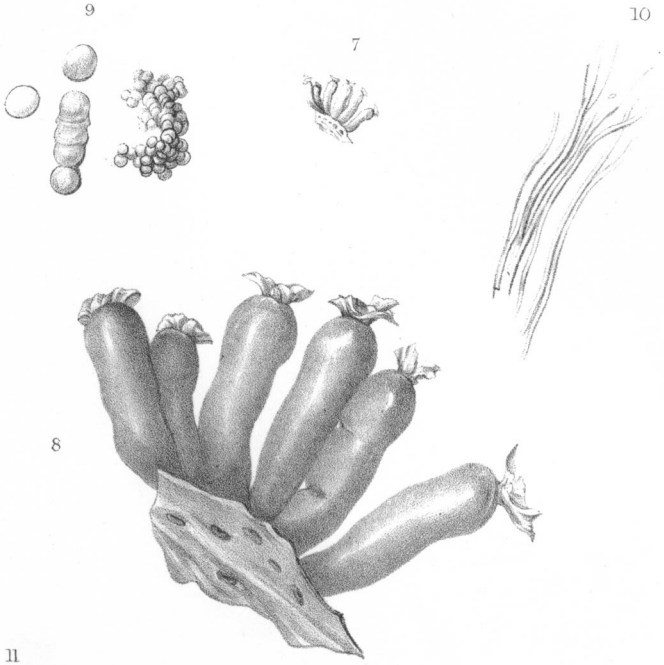


Fig. 3.

Fig. 2.

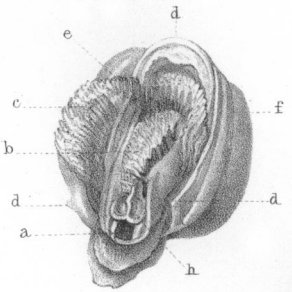


Fig. 4.

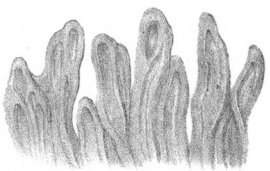


Fig. 5.

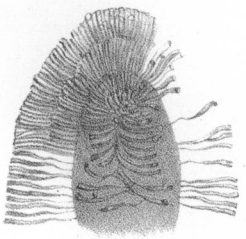


Fig. 6.